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PROLIFICATION OF THE FRUIT IN CAPSICUM AND PASSIFLORA.

BY J. ARTHUR HARRIS.

The appearance of a recent paper on the influence of cold in the production of cleistogamy and teratological phenomena in *Solanum Melongena* and in *Capsicum annuum*, by Dr. G. Mottareale,* has induced me to put into print notes and drawings made some years ago at the Missouri Botanical Garden. These observations were made upon a very large series of fruits from plants grown in the open and are consequently interesting for comparison with those studied by Mottareale. Since they refer chiefly to an anomaly which he was not able to study extensively it seems best to present the notes in full with most of the figures as originally prepared. Observations on proliferation of the fruit of *Passiflora* are also added.

CAPSICUM.

The material studied by Mottareale was grown under the following conditions. In three large greenhouses the principal plants cultivated were *Phaseolus vulgaris*, *Cucumis sativus*, *Cucurbita Pepo*, *Solanum Melongena*, *Capsicum annuum*, *C. grossum*, and *Lycopersicum esculentum*. During the early part of the winter the heating plant had not yet been installed, but owing to the mild climate the plants made a vigorous vegetative growth and were beginning to produce normal flowers when, about the middle of December, two or three nights of cold wrought havoc with them. The egg plants and the peppers lost their flowers and most of their leaves, and the more tender apical shoots blackened and dried. But the vitality of the plants was

* Mottareale, G. Ann. R. Scuola Sup. Agr., Portici. 6. 1904.
(133)

not entirely destroyed and when provision for a suitable temperature was made, the vegetative organs gradually regained their former luxuriance. But the sexual organs were very teratological in nature, and these anomalies of flower and fruit Mottareale considers the result of the conditions of temperature to which the plants were subjected.

Of the anomalies of the calyx, corolla and stamens, only pistillody of the stamens need be mentioned here. In *Capsicum* adesmy of the carpels was noted in several cases but we may confine our attention to the internal structure of the fruit. Mottareale saw diaphysis of the fruit—the production of another imperfect fruit from the center of the thalamus, and ecblastesis—the production of accessory fruits from the axils of the carpels. Both anomalies were seen in some fruits. He found the seeds either normal, abortive, more or less foliaceous, or tending to assume the form of a carpel.

The evidence for referring these anomalies to the influence of the cold seems unsatisfactory. He himself tried for two successive years to reproduce the result but without success. Furthermore, anomalies resembling those he describes are not infrequently seen in *Lycopersicum*, *Solanum* and *Capsicum*.* Confining our attention strictly to the fruit we note the occurrence of pistillody of the stamens in all three genera, the occurrence of supernumerary whorls of carpels in *Lycopersicum*, the rupturing of the fruit wall by the placentae in *Solanum Melongena*, and the production of carpel-like bodies inside the fruit of *Capsicum*.

Terracciano † observed two types of proliferation in *C. annum*. In one form the walls of the fruit, terminated by a hollow tubiform style open at the top, showed five gibbous evaginations. Internally the fruit

* Penzig, O. Pflanzen-Teratologie. 2 : 169-174. 1894.

† Terracciano, N. Nuovo Giorn. Bot. Ital. 10 : 28-34. pl. 1. 1878.

produced no seeds but contained five smaller fruits, likewise without seeds and with short styles and almost obsolete stigmas, disposed upon the apex of the thalamus. In the other type the fruits were quite normal externally and bore numerous seeds but produced also a single included fruit at the top of the axis. According to Penzig, Borbás describes central proliferation in *Capsicum*. Halsted * saw, in the same genus, a small included fruit which originated from the apex of the axis, and Viviand-Morel † figures an almost identical case, while Raymondaud ‡ also figures an internal fruit. Penzig § reports central proliferation as especially common.

In 1902 a considerable plot was devoted to the cultivation of capsicums at the Missouri Botanical Garden. Fruit-like bodies were noticed occasionally during the summer in those gathered for table use, and late in the autumn the entire crop was gathered and the fruits were dissected for the purpose of determining the frequency of the anomaly. Other material was secured for the purpose of comparison during the present year, but since it yielded only corroborative evidence and was not large enough in amount to permit of statistical discussion the following statements are based on the series collected in 1902.

From the literature cited above it seems that the carpel- or fruit-like structures may originate in three ways:— by central proliferation or diaphysis, by proliferation from the axils of the carpels or ecblastesis, and by the transformation of the primordium of an ovule into a carpellary body. All of these phenomena have been seen in other genera of plants and are to be regarded as representing valid categories, but it proved impossible to divide the anomalies

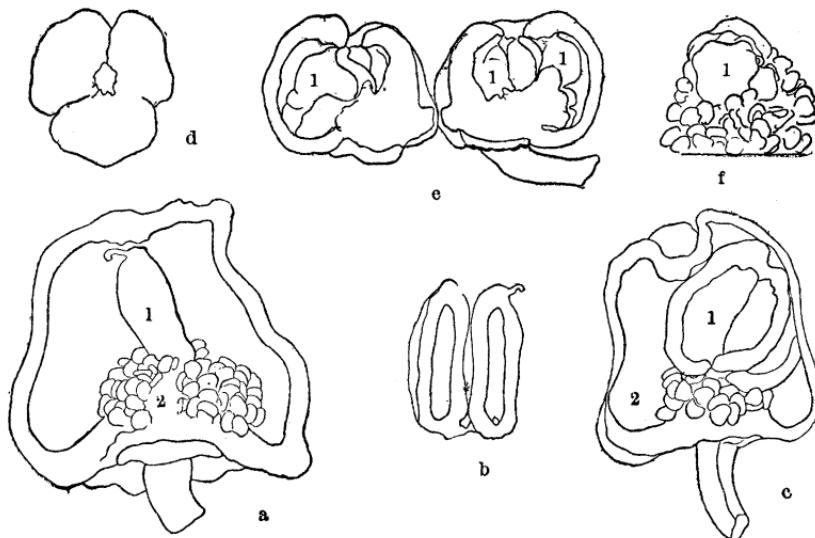
* Halsted, B. D. Bull. Torr. Bot. Club. **18**: 151. *fig.* 1891.—Pop. Sci. Mo. **42**: 321-322. *fig.* 16. 1893.

† Viviand-Morel, J. V. Lyon Horticole. **24**: 382. *fig.* 1902.

‡ Raymondaud, E. Rev. Sci. Limousin. **12**: 369-372. 1904.

§ Penzig, O. *l. c.*

found in over three hundred abnormal fruits examined into these classes. It is quite impossible to determine whether a given carpel-like body was produced from a bud in the axil of a carpel or indeed from an adventitious bud on any portion of the carpel, or from a primordium which normally would have developed into an ovule. It is no easier to ascertain whether the accessory organ was produced from the apex of the torus or from a neighboring ovule primordium. The nature of the *Capsicum* fruit precludes



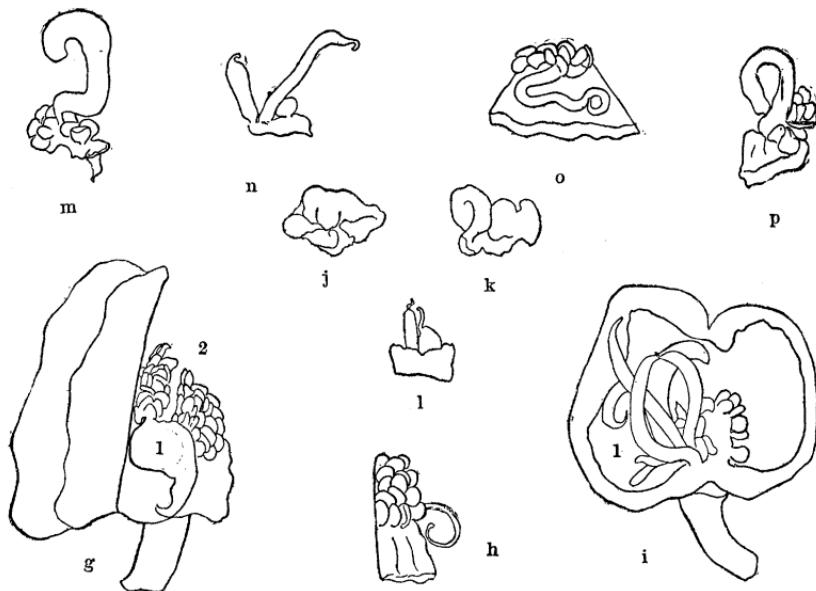
1. *CAPSICUM ANNUUM GROSSUM*, $\times \frac{1}{2}$.

the determination of some points which may be studied in other forms.

The margins of the included carpel-like bodies were in all cases completely closed, and not open as has been described in some cases of carpels produced by proliferation. The smaller ones showed no cavity whatever but were solid throughout. In form they varied from an irregularly contorted body through an almost perfectly formed sterile fruit, comparable in shape with the one in which it

was produced, to linear structures from a few millimeters to two centimeters or more in length, terminated by a minute style.

Histologically the similarity of the carpel-like bodies to the wall of the fruit is very great. Both show the exceedingly heavy epidermis and the large-celled parenchymatous ground tissue. The bodies show one or more vascular bundles similar to those of the wall of the fruit. When fresh sections are examined, numerous chromoplasts are



2. *CAPSICUM ANNUM GROSSUM* $\times \frac{1}{2}$.

seen in both but they are generally more abundant in the wall of the fruit.

Since the appearance of the teratological papers of de Vries, one of the chief objects of teratological studies is the determination of the frequency of occurrence of the various anomalies. The fruits examined by the writer belong to twenty named varieties but here only sixteen which have been described by Irish in his Revision

of the Genus *Capsicum* * or in a later paper †, will be included.

In the accompanying table the garden varieties are grouped under the botanical varieties recognized by Irish. The number of normal fruits and the number which contained carpel-like bodies, as well as the percentage which the latter are of the total number examined are given for each variety. No attempt is made to classify these bodies according to form or origin.

TABLE A. DISTRIBUTION OF ANOMALIES IN CAPSICUM.

VARIETY.	Normal.	Abnormal.	Per cent. Abnormal.
<i>Capsicum annuum acuminatum.</i>			
Chilli	105	0
Long Cayenne	200	1	.5
Long Yellow Cayenne	250	0
Yellow Nepal Chilli	176	1	.5
<i>Capsicum annuum longum.</i>			
County Fair	200	0
Long Red	165	0
<i>Capsicum annuum grossum.</i>			
Monstrous	917	167	15.4
Ruby King	40	0
Golden Dawn	73	6	7.5
Bell	89	19	17.5
Golden King	150	33	18.
Squash, or Tomato Shaped . . .	133	11	7.6
<i>Capsicum annuum abbreviatum.</i>			
Red Etna	250	0
Red Wrinkled	223	0
Burpee's Mikado	258	88	25.4
<i>Capsicum annuum cerasiforme.</i>			
Cherry	198	16	7.4
Total	3,427	342	9.

* Irish, H. C. Rept. Mo. Bot. Gard. 9: 53-110. pl. 8-28. 1899.

† Irish, H. C. Proc. Soc. Prom. Ag. Sci. 23: 63-64. 1902.

Some suggestive points are to be gathered from this table. The slender-fruited varieties classified under *C. annuum acuminatum* and *C. annuum longum* show only two cases of proliferation although nearly 1,100 fruits were dissected. Of the 2,671 fruits examined from the ten garden varieties of *C. annuum grossum*, *C. annuum abbreviatum* and *C. annuum cerasiforme*, 340, or 12.7%, show proliferation in some form. But that the relative length and diameter of the fruit is not the only factor involved is rendered probable by the three exceptions among these ten short-fruited varieties. The absence of abnormal fruits in Ruby King may be a chance result due to the small series of material examined, but this explanation cannot be offered for Etna and Red Wrinkled.

The chief conclusions to be drawn from the literature and from the present series of observations are the following.

The included bodies are doubtless formed by the three processes heretofore recognized as giving rise to intracarpellary fruits, namely diaphysis, eblastesis, and pistillody of the ovule primordium, but the fruit of *Capsicum* is not suitable for a determination of the number of cases to be referred to each category.

In form the bodies vary greatly, but two main types — rounded or irregularly contorted, and linear — are to be recognized. The more or less isodiametric form is almost invariably found at the apex of the torus or at the base of the seed-bearing region. The linear form may occupy any position.

Histologically the bodies are very similar to the wall of the fruit.

Proliferation of the fruit, using the term to cover all three phenomena mentioned above, is very common in several garden varieties of *Capsicum*. It is practically wanting in the slender-fruited forms, although some varieties form exceptions to this rule.

The foregoing facts preclude any conclusions concerning the influence of environmental conditions, until careful statistical studies have been made. These must take into consideration ancestry as well as environment.

PASSIFLORA.

A number of observations have been published on abnormal fruits in *Passiflora*, but since all the work has been done independently, I take this opportunity of bringing together the literature and of presenting further observations made upon a much larger series of material than has been examined heretofore.

Clos * describes the proliferation of the fruit of *P. gracilis*. He found two types. In one there were three pedicels each with three styles and in the other a single pedicel terminated by three styles. Salter † describes an abnormality in the ovules of *P. palmata* and *P. caerulea*. Lindberg ‡ records proliferous fruits in *P. gracilis*. His descriptions agree with those of other authors. Bernoulli § records a case of proliferation in *P. serratistipula* in which a slightly abnormal flower was produced in an apparently normal fruit. He also states that in the section Granadilla, a short, filamentous projection is frequently to be seen at the bottom of a fruit-cavity. Masters || describes a fruit of *P. quadrangularis* "wherein small flower-buds were found springing from the placentas intermixed with the seeds." Hildebrand ¶ notes fruits with

* Clos, D. Mém. Acad. Imp. Sci. Inscript. Belles-Lettres, Toulouse. V. 3: 113. 1859.

† Salter, S. I. Trans. Linn. Soc. 24: 143-150. pl. 24. 1863.

‡ Lindberg, S. O. Öfvers. Finska Vetensk.-Soc. Förh. 10: 15-16. 1867.

§ Bernoulli, G. Bot. Zeit. 27: 21-23. 1869.

|| Masters, M. T. Trans. Linn. Soc. 27: 607. 1871.

¶ Hildebrand, F. Bot. Centralbl. 9: 401-404. pl. 1. 1882.

four carpels. He figures and describes in considerable detail proliferation in fruits of *P. gracilis* in the Botanical Garden at Freiburg. He finds the produced axis bearing an indefinite number of carpels, sometimes over sixteen, having more or less completely developed stigmas and producing on their edges, which cohere in various degrees, a limited number of ovules. In several cases the main axis bore a lateral branch, which in turn produced a number of carpels of diverse degrees of development. Wigand * describes the structure of the enclosed shoot of *P. gracilis* in detail. Müller † describes briefly proliferation of the fruit of *P. alata*. In several fruits of this species he found a perfectly developed flower bud. The fruits contained an abundance of good seeds. A plant raised from these had produced, up to the time of the writing of his paper, only normal fruits.

In the summer of 1902, vigorous specimens of *P. gracilis* were growing in the Missouri Botanical Garden in part in the Cycad house and in part over a lattice in the open air. My observations are based upon the examination of 167 proliferous fruits secured by dissecting 4,240 fruits. The material was collected in four lots, the first taken from the vines growing in the greenhouse and the last three from those on the outside. Lots one and two were gathered early in October, the third was taken October 25, and the fourth lot about five days later. The distribution of the material was as follows: —

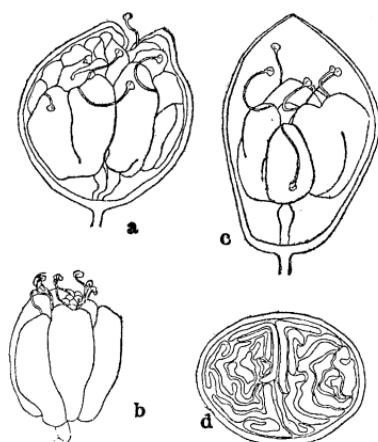
Lot I.	558 normal,	39 proliferous — 6.5 per cent.
Lot II.	1402 normal,	56 proliferous — 3.9 per cent.
Lot III.	1239 normal,	38 proliferous — 2.9 per cent.
Lot IV.	874 normal,	34 proliferous — 3.7 per cent.
Total.	4073 normal,	167 proliferous — 3.9 per cent.

* Wigand, A. Bot. Hefte. Forsch. a. d. Bot. Gart. Marburg. 2 : 125-126. 1885.

† Müller, F. Flora. 73 : 332-333. fig. 1890.

As pointed out by earlier writers, the proliferation consists in the production from the base of the fruit of a stalk, or sometimes two or more stalks bearing a variable number of carpels closely packed together as may be beautifully seen in a cross section of the fruit. The margins of the carpels are fused in various degrees or free. A few ovules are sometimes produced. For other details the accompanying figures may be consulted.

Of 125 proliferous fruits dissected, 100 had only a single central stalk while 25 had more. In several cases small bud-like or filamentous processes were seen near



3. *PASSIFLORA GRACILIS*, $\times 1$.

the base of the stalk bearing the accessory carpels, but when these produced no differentiated carpels they were not counted. The determination of the number of the included carpels is sometimes rather difficult owing to the varying degrees of fusion of the members of the outer whorls and the small size of those of the inner ones. The best criterion seems to be the number of styles. These seem to be independent of the fusion of the carpels and they are usually well developed even in the smallest members of the inner whorls. The number of carpels counted in the 25 fruits containing more than one carpel-bearing pedicel was: — 22, 22, 33, 35, 38, 42, 44, 46, 46, 46, 48, 49, 49, 51, 51, 55, 57, 64, 64, 66, 71, 72, 83, 90, 90. The number of carpels in the 100 fruits containing only a single carpel-bearing pedicel is shown in the accompanying table. The smallness of the series and the fact that the material was derived from two habitats renders any biometric discussion unprofitable.

TABLE B. NUMBER OF CARPELS IN ABNORMAL FRUITS OF PASSIFLORA.

N	F	N	F	N	F	N	F	N	F
3	3	18	3	27	1	36	3	46	2
4	18	19	2	28	1	37	4	47	1
5	3	21	4	29	4	38	2	48	1
6	8	22	2	30	1	39	2	55	1
7	3	23	1	31	3	41	3	57	1
13	1	24	2	32	1	42	1		
14	1	25	2	33	1	43	2		
15	3	26	3	34	4	45	2		

A rupturing of the wall of the fruit in the abnormal examples was very frequent, amounting to about 30% in one of the lots collected in the open. A very noticeable difference between the material growing in the greenhouse and in the open was the very much smaller size of the included group of carpels in the former. In only about 5% of the examples collected in the Cycad house was the wall of the fruit ruptured by the included body, which was usually quite small and simple, while in the material grown outside the inner group was usually large and very complicated in structure, being composed of a great number of irregularly arranged carpels.

It is interesting to note that proliferation of the fruit has been seen by three observers in another member of the Passifloraceae, *Carica Papaya*. Müller* figures a sterile fruit containing a large central fruit with numerous ovules. According to Houard,† Prain ‡ figures a specimen containing numerous secondary fruits. Urbina§ discusses an example in which the cavity in addition to the normal black seeds was filled by six conical, conduplicate

* Müller, F. l. c.

† Houard, C. Rev. Gén. Bot. 18: 131. 1906.

‡ Prain, D. Journ. As. Soc. Bengal. 1895: 196-198. pl. 4-5.

§ Urbina, M. La Naturaleza. 3: 359-360. pl. 19. 1900.

carpellary bodies of 8 to 10 centimeters in length and 4 to 6 centimeters in diameter, bearing abortive ovules. The center of the fruit was occupied by a cylindrical body of about 14 centimeters in length and 4 to 5 centimeters in diameter, bearing five branches near the base. Urbina considers this fruit to be composed of three whorls, each of five carpels. The lowermost forms the normal fruit. The second is represented by five included carpels, of which one is divided longitudinally. The third whorl, which is much more rudimentary, appears as the central column with its basal branches.

Diaphysis and ecblastesis of the fruit, while not so common as many other anomalies, need not be considered further here. The transformation of the primordium of an ovule into a carpel-like body is still rarer. The only instances known to me are the *Cheiranthus Cheiri* described by DeCandolle* and Masters,† the Barbarossa grape figured by Masters,‡ the *Sinapis arvensis* described by Baillon,§ and the *Dianthus* figured by Berkeley.|| A careful search through the older discussions of the evidence of teratology on the homologies of the ovule would, perhaps, disclose other cases.

Such anomalies as the present ones are interesting in connection with Sach's theory of "material and form," to which Goebel is inclined to attach much significance.

* DeCandolle, A. P. and A. DeCandolle. *Nouv. Mém. Soc. Helv. Sci. Nat.* **5**. *pl. 5*. 1841.

† Masters, M. T. *Veg. Ter.* 182. *fig. 94-95.* 1869.

‡ Masters, M. T. *l. c.* 182-183. *fig. 96-97.*

§ Baillon, H. *Adansonia.* **3**: 351-353. *pl. 12.* 1862-'63.

|| Berkeley, M. J. *Gard. Chron.* **1850**: 612. *figures.*

EXPLANATION OF TEXT FIGURES.

All of the figures are diagrammatic.

Figure 1.—*Capsicum annuum grossum*. a—c, "Monstrous." d—e, "Golden King." f, "Bell." In a and c the carpel-like bodies (1), seen at the apex of the torus surrounded by seeds (2), probably originated by central proliferation. In b the body from a is seen in longitudinal section, showing the thickness of the walls. In c is also to be seen a carpel-like body (3), probably originating by pistillody of an ovule. Slight adesmy of the carpels is represented, from above, in d, and in longitudinal section in the two halves of the same fruit, in e. The torus of this fruit was abnormally large and almost the entire cavity of the fruit was filled with large, irregularly rounded fruit-like bodies (1). The origin of these bodies is uncertain. In f an irregularly rounded fruit-like structure (1) is seen at the apex of the torus surrounded by seeds.

Figure 2.—*Capsicum annuum grossum*. g—h, "Bell." i—l, "Golden King." m—n, "Monstrous." o—p, "Bell." In g half of the fruit wall is removed to show the torus bearing seeds (2), and a large flattened carpel-like body (1), originating by ecblastesis or by pistillody of an ovule. In h the same condition prevails but here the body is linear. In i seven linear bodies (1), originating by ecblastesis or by pistillody of ovules, are seen. j—k represent various forms of carpel-like bodies removed from the fruits, sometimes with a block of the torus.

Figure 3.—Central proliferation of the fruits in *Passiflora gracilis*. a, Fruit with two carpel-bearing pedicels. b, Carpel-bearing pedicel removed from fruit. c, Fruit with single included pedicel. d, Diagram of cross section of fruit, with two carpel-bearing pedicels, such as is shown in a, showing irregular arrangement of included carpels.